MATERNAL BEHAVIOR IN RABBITS: REGULATION BY HORMONAL AND SENSORY FACTORS

GABRIELA GONZÁLEZ-MARISCAL

Centro de Investigación en Reproducción Animal, CINVESTAV-UAT.
Apdo Postal 62. Tlaxcala, Tlax. 90000, Mexico.
gglezm@prodigy.net.mx

ABSTRACT

Maternal behavior in rabbits involves building a nest of straw and body hair inside an underground burrow, before parturition, and the display of a single, brief (ca. 3 min.), nursing bout per day throughout lactation. The onset and decline of digging, straw-carrying, and hair-pulling is controlled by specific combinations of estradiol, progesterone, testosterone, and prolactin (PRL). These hormones also prime the maternal brain to respond effectively to the newborn pups: antagonizing the release of PRL that occurs before parturition (by injecting bromocryptine s.c.) abolishes maternal behavior in most rabbits. This effect is counteracted by the intracerebroventricular administration of rabbit PRL. We have investigated the brain areas involved in regulating specific aspects of maternal behavior by: a) determining the distribution of receptors for estradiol (ER-alpha) and progesterone (PR); b) implanting estradiol in the forebrain and quantifying the display of nest-building; c) establishing the expression of an immediate early gene (*c-fos*) in association with the display of maternal behavior. These studies have revealed that specific forebrain regions (e.g., the preoptic area and septum) play a major role in the control of nest-building and maternal responsiveness: they are rich in ER-alpha and PR; implants of estradiol benzoate stimulate digging and straw-carrying in ovariectomized rabbits treated with progesterone s.c.; an increase in the number of *c-fos* immunoreactive neurons is observed following nursing. In addition to hormonal stimulation, the adequate display of maternal behavior relies heavily on the perception of stimuli coming from the young. By preventing mother/young contact at parturition or during early lactation maternal responsiveness is altered or abolished. Suckling stimulation *per se* is not essential to maintain maternal behavior as mothers deprived of nipples (i.e., thelectomized) are responsive to the young. However, the duration of the mother/young interaction is greatly extended in thelectomized females and also in mothers whose nipples have been covered with cushions. Moreover, decreasing the amount of suckling stimulation (by providing only one pup) or providing a litter that is unable to suckle (by placing adhesive tape over the mouths) also extends the time mothers spend with the young inside the nest box. These results show a major role of suckling stimulation in timing the duration of mother/young contact. In summary, the behavior of mother rabbits is regulated by a multiplicity of hormonal and somatosensory stimuli that act in concert to determine the onset, offset and duration of specific maternal activities.

Key words: maternal behavior, nest-building, steroid hormones, prolactin, suckling.

INTRODUCTION

Maternal behavior in rabbits begins in late pregnancy as the female constructs a nest of straw and body hair inside a burrow (GONZÁLEZ-MARISCAL *et al.* 1994b; ROSS *et al.* 1963). We have evidence that maternal nest-building is regulated by the action of estradiol (E), progesterone (P), testosterone, and prolactin (PRL; GONZÁLEZ-MARISCAL *et al.* 1994b, 1996, 2003). Thus, digging is maximally expressed between days 25-27 of pregnancy, when circulating levels of E and P are high (60 pg/ml and 9 ng/ml, respectively). Straw-carrying occurs across prepartum days 3 to 1 (coinciding with a decrease in digging), as the concentration of P declines and E rises (75 pg/ml). Hair-plucking (preceded by the loosening of body hair) occurs from the day of parturition into lactation days 3-4, when P levels are negligible and high levels of testosterone (308 pg/ml) and PRL (160 ng/ml) are observed (Figure 1).

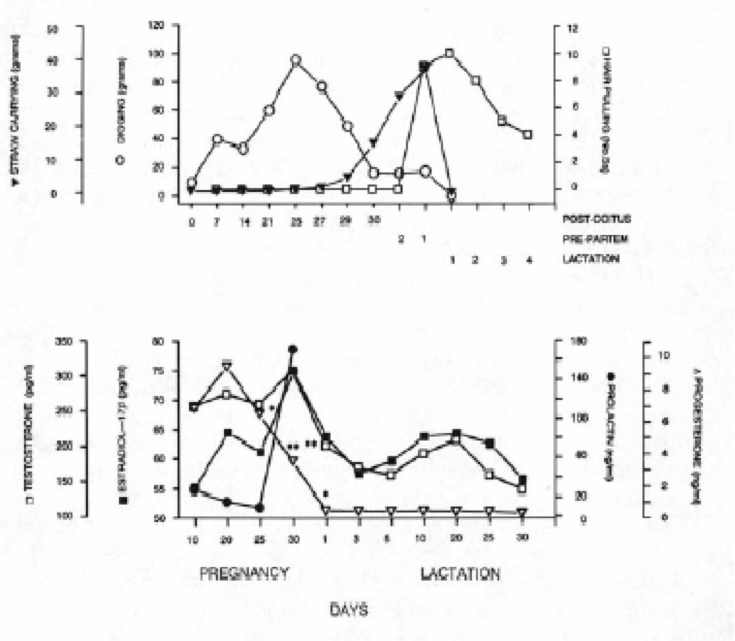

Figure 1. Upper panel: Quantification of digging, straw-carrying, and hair-pulling across pregnancy. Lower panel: Variations in the concentration of estradiol 17-beta, progesterone, testosterone, and prolactin in the blood throughout pregnancy and lactation. From: GONZÁLEZ-MARISCAL *et al.* 1994b.

In ovariectomized (ovx) females the combined injection of estradiol benzoate (EB; 5 micrograms/day) and P (10 mg/day) consistently stimulates digging, while the withdrawal of P (and continuation of EB) allows the expression of straw-carrying and hair-pulling and also provokes a decline in digging (Figure 2; GONZÁLEZ-MARISCAL *et al.* 1996).

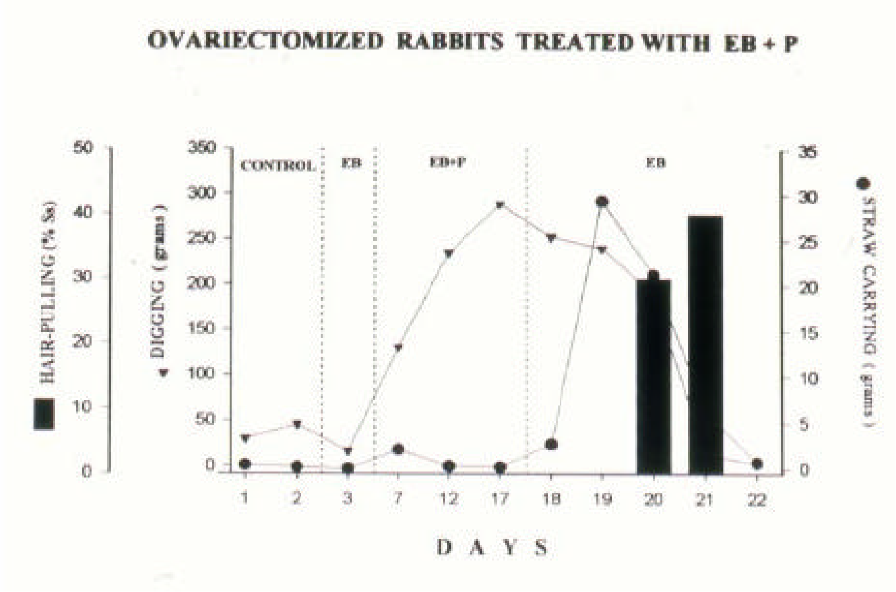

Figure 2. Stimulation of nest-building in ovariectomized rabbits by the injection of estradiol benzoate (EB; 5 micrograms/day) and progesterone (P; 10 mg/day). Note that digging was expressed when both steroids were present and declined after P withdrawal. This, in turn, stimulated straw-carrying followed by hair-pulling. From: GONZÁLEZ-MARISCAL, ROSENBLATT 1996.

Hair-loosening is induced in ovx rabbits by the injection of either testosterone propionate or 5-alpha-dihydrotestosterone propionate (5 mg/day; GONZÁLEZ-MARISCAL *et al.* 2003c). In addition to gonadal steroids there is evidence that PRL promotes maternal nest-building. Thus: a) in ovx rabbits given EB and P to stimulate nest-building, P withdrawal leads to PRL release (GONZÁLEZ-MARISCAL *et al.* 1996); b) injections of bromocryptine (a dopamine agonist; MARTIN and BATESON 1982; MELTZER *et al.* 1982) together with the steroid treatment prevent PRL release provoked by P withdrawal in ovx rabbits (GONZÁLEZ-MARISCAL *et al.* 1996); c) high concentrations of PRL are detected in blood shortly before parturition (GONZÁLEZ-MARISCAL *et al*. 2000; MCNEILLY, FRIESEN 1978; NEGATU, MCNITT 2002); d) bromocryptine antagonizes nest-building when injected in late pregnancy (GONZÁLEZ-MARISCAL *et al.* 2000); e) the intracerebroventricular injection of rabbit PRL reverses the antagonistic effect of bromocryptine on nest-building (GONZÁLEZ-MARISCAL *et al.* 2003b; see Table 1).

In contrast with the elaborate process of nest-building that occurs in late pregnancy, following parturition maternal behavior consists of a single nursing bout per day lasting around three min (DREWETT *et al.* 1982; GONZÁLEZ-MARISCAL *et al*. 1994; LINCOLN 1974) and displayed with circadian periodicity (JILGE 1993, 1995). The rabbit pups can locate the mother's nipples and suckle milk within such a short time due to the perception of an olfactory cue that is emitted through the doe's nipples (HUDSON, DISTEL 1983). This so-called "mammary pheromone" was recently characterized as a single compound: 2-methylbut-2-enal (SCHAAL *et al.* 2003). Its emission is stimulated by E, P, and PRL as daily injections of EB+P stimulate mammary pheromone in ovx rabbits while P withdrawal leads to a decline in this process (HUDSON *et al*. 1990; Figure 3). Maximal levels of mammary pheromone emission can be maintained despite P withdrawal by injecting PRL (GONZÁLEZ-MARISCAL *et al.* 1994a; Figure 3).

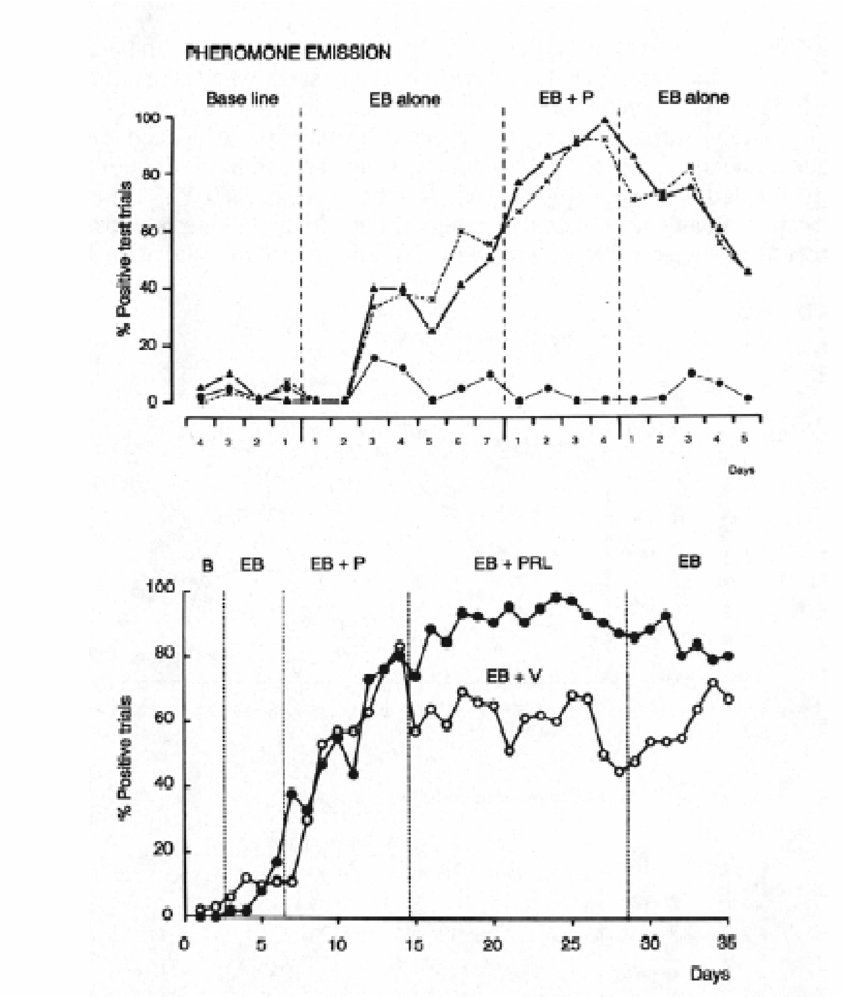

Figure 3. Upper panel: In ovariectomized (ovx) rabbits the combined injection of estradiol benzoate (EB; 1 or 10 micrograms/day) plus progesterone (P; 10 mg/day) induces maximal levels of mammary pheromone emission. A decline is observed following P withdrawal. From HUDSON *et al.* 1990. Lower panel: In ovx rabbits primed with EB plus P the combined injection of EB (0.5 micrograms/day) plus ovine prolactin (PRL; 1.5 mg/day) maintains maximal levels of mammary pheromone emission despite P withdrawal. From GONZÁLEZ-MARISCAL *et al.* 1994a.

The evidence presented so far shows that steroid hormones and PRL participate in regulating the onset/offset of specific activities of the nest-building process. Yet, the hormonal profile characteristic of pregnancy changes dramatically in the pre-partum period and across lactation. Specifically, as parturition approaches, E rises and P declines (GONZÁLEZ-MARISCAL *et al.* 1994b), while oxytocin (FUCHS, DAWOOD 1980) and PRL (GONZÁLEZ-MARISCAL *et al.* 2000; MC NEILLY, FRIESEN 1978; NEGATU, MC NITT 2002) are released shortly before delivery. Across lactation, E is present at lower concentrations than in late pregnancy and P is absent (GONZÁLEZ-MARISCAL *et al.* 1994b), while oxytocin and PRL are released at each nursing bout (FUCHS *et al.* 1984). The impact of such changes in the endocrine milieu for the display of pup-directed maternal behavior will be discussed in the following section.

SOMATOSENSORY STIMULI AND HORMONAL FACTORS PROMOTE AND MAINTAIN MATERNAL RESPONSIVENESS

Parturition in rabbits is brief (ca. 10 min; HUDSON *et al.* 1999) and it is preceded by a massive release of oxytocin and PRL (see previous section). We have obtained evidence that, by acting on the brain in late pregnancy, PRL promotes maternal responsiveness to the young. Thus, injections of bromocryptine from pregnancy day 26 to parturition reduce the incidence of maternal behavior (i.e., entrance into the nest box and adoption of a crouching posture over the litter; GONZÁLEZ-MARISCAL *et al.* 2000, 2003b). This effect is counteracted by the simultaneous injection of rabbit PRL into the cerebral ventricles (GONZÁLEZ-MARISCAL *et al.* 2003b). Across the first week of lactation this group of experimental animals showed a behavior that was not significantly different from that observed in the control group (injected with vehicle), i.e.: rapid entrance into the nest box, crouching over the litter, and allowing the young to suckle, although milk output was reduced (due to the previous injections of bromocryptine).

Table 1: Intracerebroventricular (icv) injections of rabbit prolactin reverse the disruptive effects of bromocryptine on nest-building and maternal behavior

Group	% females with nest	% maternal females
Control (vehicle sc + vehicle icv)	77	77
Bromocryptine sc + vehicle icv	19*	19*
Bromocryptine sc + rabbit PRL icv	93	57

*p<0.05 vs control group

In addition to PRL, acting on the brain before parturition, we have evidence that somatosensory stimuli received by the mother rabbit at delivery and during the first week post-partum are essential for the adequate expression of maternal care. If pups are removed as they are being born, thus preventing the mother from having any contact with them, maternal behavior is abolished in 66% of cases (GONZÁLEZ-MARISCAL *et al.* 1998). These results indicate that as yet undetermined stimuli, received at a critical time point (the peripartum period), are necessary to allow the maternal brain (previously primed with steroid hormones and PRL) to respond adequately to the newborn. Yet, those stimuli are insufficient for such purpose as rabbits allowed to interact with the litter at delivery but anesthetized at each nursing bout across lactation days 1-7 (a procedure that prevents the conscious contact between mother and young) show aberrant maternal behavior in 60% of cases on the days following anesthesia withdrawal. If this procedure is performed in mid-lactation it has no effect on maternal behavior (GONZÁLEZ-MARISCAL *et al.* 1998). Interestingly, nipple stimulation *per se* seems not to play a major role in maintaining maternal behavior as 70% of females whose nipples were removed (thelectomized) before mating showed a normal responsiveness to the newborn, readily entered the nest box for at least 7 days postpartum, and crouched over the litter even though suckling could not occur (GONZÁLEZ-MARISCAL *et al.* 2000). Taken together, the above results indicate that specific hormones and somatosensory stimuli participate in regulating the expression of maternal responsiveness. In the following sections we will present the experimental strategies we have used to investigate specific aspects of such multifactorial control of rabbit maternal behavior.

STEROID ACTIONS ON THE MATERNAL BRAIN

As described in earlier sections, E and P are key hormones that determine the onset/offset of specific activities of the nest-building process. Therefore, establishing where these hormones act on the maternal brain is essential for understanding the neuroendocrine regulation of this complex mammalian behavior. By means of immunocytochemistry we have explored the distribution of estrogen receptor (ER) alpha and progesterone receptor (PR) in female rabbits. We have found high concentrations of both receptors in specific regions of the brain, notably the preoptic area (Figure 4).

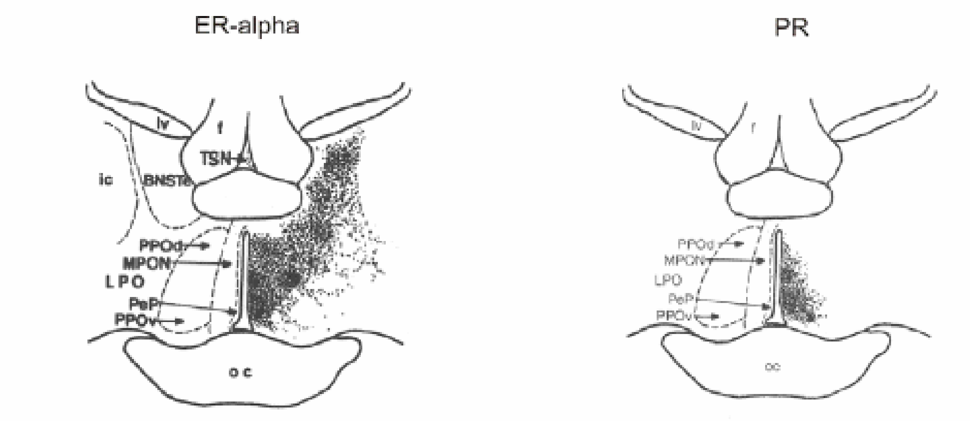

Figure 4. Left panel: Distribution of estrogen receptor-alpha immunoreactive neurons in the preoptic region of an ovariectomized rabbit. Note the high density observed in the bed nucleus of the stria terminalis (BNST) and also in three preoptic nuclei: medial (MPON), principal (dorsal and ventral subdivisions; PPOd, PPOv), and periventricular (PeP). From: CABA *et al.* 2003a. Right panel: Distribution of progesterone receptor immunoreactive neurons in the preoptic region of an ovariectomized rabbit treated with estradiol benzoate. Note the high concentration observed in the same three preoptic nuclei specified above. From: CABA *et al.* 2003b.

This region has a well-established participation in the control of maternal behavior in rodents (for reviews see: GONZÁLEZ-MARISCAL, POINDRON 2002; NUMAN, INSEL 2003). In addition to the preoptic region ER alpha is widely distributed in the forebrain, e.g.: bed nucleus of the stria terminalis, nucleus accumbens, paraventricular nucleus, ventrolateral hypothalamus, amygdala, and subiculum (CABA *et al.* 2003a). PR, in contrast, has a more restricted distribution: aside from the preoptic region and infundibular nucleus it is found only in the paraventicular nucleus and the ventrolateral hypothalamus (CABA *et al.* 2003b). From these findings we investigated the effect of implanting estradiol benzoate (EB) into the preoptic region of ovx rabbits treated s.c. with P. We found that females implanted with EB in the preoptic region showed a gradual increase in digging for as long as P was injected s.c. The removal of this hormone provoked a decline in digging and an onset of straw-carrying (GONZÁLEZ-MARISCAL *et al.* 2003a; Figure 5). Females implanted with cholesterol in the preoptic region and given P s.c. failed to show these responses (data not shown).

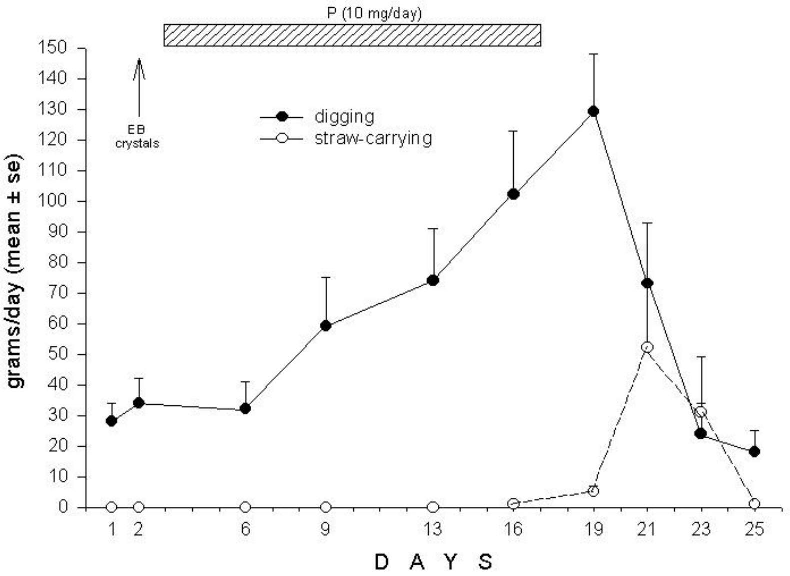

Figure 5. Stimulation of digging in ovariectomized rabbits by implanting estradiol benzoate (EB) into the preoptic region and injecting progesterone (P; 10 mg/day) s.c. Note the decline in digging and onset of straw carrying following P withdrawal.

These results indicate that the action of estradiol on the preoptic region is necessary and sufficient to allow P to facilitate digging and straw-carrying by as yet undetermined mechanisms.

BRAIN REGIONS POSSIBLY INVOLVED IN REGULATING MOTHER-YOUNG INTERACTIONS

Little is known about the brain structures involved in the many features characteristic of maternal behavior in rabbits, e.g.: motivation to respond to the young, adoption of a crouching posture over the litter, milk output, duration of the suckling episode, etc. To begin investigating this matter CRUZ and BEYER (1972) placed electrolytic lesions in the septum and nucleus accumbens of pregnant rabbits and found that nest-building and nursing behavior were disrupted. From this finding we investigated if such brain areas become activated after the display of maternal behavior. The detection of the *c-fos* protein, by means of immunocytochemistry, has been widely used to quantify changes in brain activity provoked by a variety of stimuli (olfactory, visual, tactile; for review see MORGAN, CURRAN 1991). We sacrificed mother rabbits after nursing on lactation day 7, quantified the number of *c-fos* immunoreactive (IR) cells in specific brain regions, and compared these results with those obtained in mothers not given pups for nursing on such day (GONZÁLEZ-MARISCAL *et al.* 2002). We found a significantly larger number of *c-fos*-IR cells in females that nursed in: the lateral septum, the bed nucleus of the stria terminalis, and the paraventricular and supraoptic nuclei (Table 2).

Table 2. Effect of nursing on the number of *c-fos* immunoreactive cells (mean±se) in specific brain regions

Brain region	Condition	
	Nursing	No Nursing
Lateral septum	316±78**	82±22
Bed nucleus of the stria terminalis	344±58$^+$	151±51
Supraoptic nucleus	208±42*	57±17
Paraventricular nucleus	398±36**	141±40

*p<0.05, $^+$p<0.02, **p<0.01 vs no nursing

Other regions (e.g., ventromedial hypothalamic nucleus, lateral habenula, suprachiasmatic nucleus) did not show significant differences between nursing and non-nursing rabbits (data not shown). These results indicate that the mother-young interaction activates areas involved in the milk ejection reflex (i.e., paraventricular and supraoptic nuclei) and also others (e.g., septum, bed nucleus of the stria terminalis) that may participate in the control of additional aspects of maternal behavior. As these data coincide with those obtained in the lesion study described above (CRUZ, BEYER 1972) they suggest that the region of the septum-bed nucleus of the stria terminalis is essential for the normal display of maternal behavior.

SUCKLING STIMULATION REGULATES THE DURATION OF MOTHER-YOUNG CONTACT

One characteristic feature of rabbit maternal behavior is the constant duration of the single, daily nursing bout. A number of investigators have independently confirmed that it lasts around three min, regardless of the day of lactation (DREWETT *et al.* 1982; GONZÁLEZ-MARISCAL *et al*. 1994; LINCOLN 1974; ZARROW *et al.* 1965). The mechanisms that regulate this apparently invariable duration of nursing are unknown. Yet, FINDLAY and TALLAL (1971) briefly reported that mothers given only two pups showed longer nursing episodes than did rabbits with larger litters. We have found (GONZÁLEZ-MARISCAL *et al*. 2000) that thelectomized mothers show maternal behavior towards the litter and crouch over the young despite their incapacity to nurse. Yet, thelectomized mothers stay inside the nest box with the litter for a longer time than do nursing rabbits. Moreover, mothers injected with bromocryptine (a dopamine agonist that prevents the release of PRL) in early lactation show a reduced milk output and a longer time inside the nest box with the litter (GONZÁLEZ-MARISCAL *et al*. 2000). The above results suggest that stimuli related with suckling stimulation and milk output regulate the duration of the nursing bout. To explore this possibility we investigated the effect of altering the suckling stimulation received by mother rabbits on the duration of the nursing bout (GONZÁLEZ-MARISCAL, CUAMATZI 2003). We found that mothers given 1 pup stayed inside the nest box for a significantly longer time (11.0±1.7 min) than did rabbits provided with 8 young (3.9±0.1 min; $p<0.001$). Placing cushions over the nipples, a procedure that allowed mothers to receive tactile stimulation from the litter but prevented suckling, also extended the time inside the nest box, from 4.5±0.5 min to 7.9±1.1 min ($p=0.01$). Covering the pup's mouths with adhesive tape to prevent them from suckling (but otherwise allowing them to provide tactile stimulation to the mother's ventrum) provoked the same effect: time inside the nest box increased from 4.1±0.3 to 9.4±2.5 min ($p<0.05$). Taken together, this evidence indicates that suckling stimulation plays a major role in timing the duration of the mother-young contact in rabbits.

CONCLUSION

The maternal behavior of rabbits shows features that distinguish it from that of most studied mammals, i.e.: the construction of an elaborate nest before parturition and a very brief contact with the young across lactation. Yet, it seems that rabbits rely on the same factors (hormonal and sensory) as other mammals to regulate the expression of the behavioral patterns that are appropriate for these animals. The specific characteristics of such behaviors (e.g., fixed duration of the nursing bout, circadian periodicity) indicate an elaborate neurobiological control and, therefore, offer the possibility of using them as models for exploring more general principles in nervous system function. The introduction of new animal models in biology will enrich our understanding of the strategies evolved by mammals to adapt to a changing environment and to increase their distribution on the planet. The knowledge derived from studying the reproductive behavior of rabbits can have a direct impact on the way we raise and care for these animals in the farm and the laboratory, in our homes and in the wild.

REFERENCES

CABA M., BEYER C., GONZÁLEZ-MARISCAL G., MORRELL J.I. 2003a. Immunocytochemical detection of estrogen receptor alpha in the female rabbit forebrain: topography and regulation by estradiol. *Neuroendocrinology* **77**:208-222.

CABA M., ROVIROSA M.J., BEYER C., GONZÁLEZ-MARISCAL G. 2003b. Immunocytochemical detection of progesterone receptor in the female rabbit forebrain: distribution and regulation by oestradiol and progesterone. *J. Neuroendocrinol.* **15**:855-864.

CRUZ M.L., BEYER C. 1972. Effects of septal lesions on maternal behavior and lactation in the rabbit. *Physiol. Behav.* **9**:361-365.

DREWETT R.F., KENDRICK K.M., SANDERS D.J., TREW A.M. 1982. A quantitative analysis of the feeding behavior of suckling rabbits. *Dev. Psychobiol.* **15**:25-32.

FINDLAY A.L.R., TALLAL P.A. 1971. Effect of reduced suckling stimulation on the duration of nursing in the rabbit. *J. Comp. Physiol. Psychol.* **76**:236-241.

FUCHS A.R., CUBILE L., DAWOOD M.Y., JORGENSEN F.S. 1984. Release of oxytocin and prolactin by suckling rabbits throughout lactation. *Endocrinology* **114**:462-469.

FUCHS A.R., DAWOOD M.Y. 1980. Oxytocin release and uterine activation during parturition in rabbits. *Endocrinology* **107**:1117-1126.

GONZÁLEZ-MARISCAL G., CHIRINO R., BEYER C., ROSENBLATT J.S. 2003a. Forebrain implants of estradiol stimulate specific aspects of maternal nest-building in ovariectomized rabbits. Submitted to: *Horm. Behav.*

GONZÁLEZ-MARISCAL G., CHIRINO R., FLORES-ALONSO J.C., BEYER C., ROSENBLATT J.S. 2003b. Reversal of the inhibitory effect of bromocryptine on rabbit maternal behavior by ICV injections of prolactin (PRL) in late pregnancy. *Horm. Behav.* **44**:52. Abstr. 142.

GONZÁLEZ-MARISCAL G., CHIRINO R., HUDSON R. 1994a. Prolactin stimulates emission of nipple pheromone in ovariectomized New Zealand white rabbits. *Biol. Reprod.* **50**:373-376.

González-Mariscal G., Cuamatzi E. 2003. Number of suckling pups determines duration of mother-young contact across early lactation in rabbits. *Dev. Psychobiol.* **43**:256. Abstr. 51.

GONZÁLEZ-MARISCAL G., DÍAZ-SÁNCHEZ V., MELO A.I., BEYER C., ROSENBLATT J.S. 1994b. Maternal behavior in New Zealand white rabbits: quantification of somatic events, motor patterns and steroid plasma levels. *Physiol. Behav.* **55**:1081-1089.

GONZÁLEZ-MARISCAL G., JIMÉNEZ A., BEYER C. 2002. Once-a-day suckling activates c -fos in specific areas of the rabbit forebrain: effect of reducing inter-suckling interval. *Horm. Behav.* **41**:468. Abstr. 141.

GONZÁLEZ-MARISCAL G., JIMÉNEZ P., BEYER C., ROSENBLATT J.S. 2003c. Androgens stimulate specific aspects of maternal nest-building and reduce food intake in rabbits. *Horm. Behav.* **43**:312-317.

GONZÁLEZ-MARISCAL G., MELO A.I., CHIRINO R., JIMÉNEZ P., BEYER C., ROSENBLATT J.S. 1998. Importance of mother/young contact at parturition and across early lactation for the expression of maternal behavior in rabbits. *Dev. Psychobiol.* **32**:101-111.

GONZÁLEZ-MARISCAL G., MELO A.I., JIMÉNEZ P., BEYER C., ROSENBLATT J.S. 1996. Estradiol, progesterone, and prolactin regulate maternal nest-building in rabbits. *J. Neuroendocrinol.* **8**:901-907.

GONZÁLEZ-MARISCAL G., MELO A.I., PARLOW A.F., BEYER C., ROSENBLATT J.S. 2000. Pharmacological evidence that prolactin acts from late gestation to promote maternal behaviour in rabbits. *J. Neuroendocrinol.* **12**:983-992.

GONZÁLEZ-MARISCAL G., POINDRON P. 2002. Parental care in mammals: immediate internal and sensory factors of control. In: *Hormones, Brain and Behavior.* (Edit. Pfaff, D., Arnold, A.P., Etgen, A.M., Fahrbach, S.E., Rubin, R.T.), Academic Press, pp 215-298.

GONZÁLEZ-MARISCAL G., ROSENBLATT J.S. 1996. Maternal behavior in rabbits. A historical and multidisciplinary perspective. In: *Parental care: evolution, mechanisms and adaptive significance.* (Edit. Rosenblatt, J.S., Snowdon, C.T.), Academic Press, pp 333-360.

HUDSON R., CRUZ Y., LUCIO R.A., NINOMIYA J., MARTÍNEZ-GÓMEZ, M. 1999. Temporal patterning of parturition in rabbits and rats. *Physiol. Behav.* **66**:599-604.

HUDSON R., DISTEL H. 1983. Nipple location by newborn rabbits: behavioral evidence for pheromonal guidance. *Behaviour* **85**:260-275.

HUDSON R., GONZÁLEZ-MARISCAL G., BEYER C. 1990. Chin-marking behavior, sexual receptivity, and pheromone emission in steroid-treated, ovariectomized rabbits. *Horm. Behav.* **24**:1-13.

JILGE B. 1993. The ontogeny of circadian rhythms in the rabbit. *J. Biol. Rhythms* **8**:247-260.

JILGE B. 1995. Ontogeny of the rabbit's circadian rhythms without an external zeitgeber. *Physiol. Behav.* **58**:131-140.

LINCOLN D.W. 1974. Suckling: a time constant in the nursing behavior of the rabbit. *Physiol. Behav.* **13**:711-714.

MARTIN P., BATESON P. 1982. The lactation-blocking drug bromocriptine and its application to studies of weaning and behavioral development. *Dev. Psychobiol.* **15**:139-157.

MC NEILLY A.S., FRIESEN H.G.1978. Prolactin during pregnancy and lactation in the rabbit. *Endocrinology* **102**:1548-1554.

MELTZER H.Y., GUDELSKI G.A., SIMONOVIC M., FANG V.S. 1982. Effect of dopamine agonists and antagonists on prolactin and growth hormone secretion. *Psychopharmacology* **28**:200-218.

MORGAN J.I., CURRAN T. 1991. Stimulus-transcription coupling in the nervous system: involvement of the inducible proto-oncogenes fos and jun. *Annu. Rev. Neurosci.* **14**:421-451.

NEGATU Z., MC NITT J.I. 2002. Hormone profiles and nest-building behavior during the periparturient period in rabbit does. *Anim. Reprod. Sci.* **92**:125-135.

Numan M., Insel T.R. 2003. The neurobiology of parental behavior. Springer, New York.

ROSS S., ZARROW M.X., SAWIN P.B., DENENBERG V.H., BLUMENFIELD M. 1963. Maternal behaviour in the rabbit under semi-natural conditions. *Anim. Behav.* **11**:283-285.

SCHAAL B., COUREAUD G., LANGLOIS D., GINIES C., SPEMON E., PERRIER G. 2003. The mammary pheromone of the rabbit: chemical and behavioural characterization. *Nature* **424**:68-72.

ZARROW M.X., DENENBERG V.H., ANDERSON C.O. 1965. Rabbit: frequency of suckling in the pup. *Science* **150**:1835-1836.